NOTE ON THE ANATOMY OF *VOLUTA ANCILLA* (Sol.), *NEPTUNEOPSIS GILCHRISTI*, Sby., AND *VOLUTILITHES ABYSSICOLA* (Ad. & Rve.).

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PLATE X.

Through the kindness of Mr. G. B. Sowerby, I have received the soft parts of two very interesting molluscs, viz., *Neptuneopsis Gilchristi*, Sby., and *Volutilithes abyssicola* (Ad. & Rve.), neither of which have been previously obtained. Since these two molluscs present a number of interesting features, I have appended a fairly exhaustive account of their anatomy, and for comparison have given also a description of *Voluta* (*Cymbiola*) *ancilla* (Sol.), two specimens of which were kindly placed at my disposal by Mr. E. A. Smith.

Our knowledge of the anatomy of the Volutidæ is very meagre, and, save for two accounts, is practically confined to the external form and to the radula. We are, however, indebted to Quoy & Gaimard[1] and Bouvier[2] for some anatomical information on this family, though unfortunately the figures of the first-named observers are so lacking in detail and, I am afraid, in accuracy as to be practically worthless. Bouvier's account, on the other hand, is very precise, and in it he deals largely with the nervous system, but also describes the salivary glands and some other organs. The form which he examined, *V. Neptuni*, Gmelin, is, however, not a true Volute, but belongs to the genus *Melo*. Unfortunately, the form which I am describing, *Voluta ancilla* (Sol.), though a Volute, is to be referred to the subgenus *Cymbiola*, so that a description of the anatomy of the type of the genus *Voluta* is still wanting.

A short summary of results of my observations on *Neptuneopsis* has already appeared,[3] but the published account is much condensed, and since it requires some correction I have taken the opportunity while describing *Volutilithes* and *Voluta* to give a fuller description of the anatomy of this curious form. The example of *Neptuneopsis* and the *Volutilithes* are some of the first-fruits of the marine investigations now being carried on at the Cape of Good Hope, and judging from these early samples we may safely prophesy a great increase to our knowledge of malacology, especially because those in charge of the investigations are preserving the animal as well as the shells.

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[1] Voyage de l'Astrolabe, vol. ii, pp. 621–632, and pl. xliv, figs. 9–11.

[2] Ann. Sci. Nat., Zool., sér. vii, tom. iii, pp. 301–306; and Bull. Soc. Philom. Paris, sér. vii, tom. xi, p. 102.

[3] Marine Investigations in South Africa: Department Agriculture, Cape of Good Hope, No. 5, 1898.

The *Neptuneopsis* was well preserved in spirit, but the *Volutilithes* was still more admirably preserved in an extended condition in formol, an ideal medium for specimens for dissection.

1. Voluta (Cymbiola) ancilla (Sol.).

The *external characters* of this Volute are precisely similar to those of *V.* (*Vespertilio*) *vespertilio*, Linn., and *V.* (*Alcithoe*) *Pacifica*, Sol., as figured by Quoy & Gaimard, the most notable feature being the curiously flattened and expanded head and the appendices to the siphon (Pl. X, Fig. 1).

The pallial complex.—Of the two specimens examined one was a male and the other a female, the former showing a moderately developed, grooved penis, situated just behind the right head-lobe; a long groove led up to the opening of the vas-deferens high up in the mantle-cavity. In the female a large, swollen, glandular oviduct opened close to the anus.

The gill, as in other Rhachiglossa, consists of triangular plates, and in this respect the Rhachiglossa appear more primitive than the Tænioglossa. Similarly, the osphradium is large and bipectinate,[1] the hypobranchial mucous gland very conspicuous, and resembling that of *Buccinum*; the renal aperture is also very prominent. (Pl. X, Fig. 1.)

The alimentary canal.—The mouth opens on the end of a moderately developed introvert. The buccal mass is conspicuous, and the radula-sac large. From the dorsal surface of the former the œsophagus originates; this is a very muscular tube, which changes its character abruptly shortly after emerging from the introvert. At this point the œsophagus appears to be temporarily enlarged and to be more muscular, but it rapidly diminishes again, and its walls no longer appear conspicuously muscular. The œsophagus (*œ.*) passes up over the columella muscle, becomes slightly dilated, and then suddenly constricted before opening into the stomach. The stomach (*st.*), which is a slightly enlarged portion of the gut, is characterized by the conspicuous folding of its wall and by the opening of the bile-duct; it passes imperceptibly into the intestine. The whole alimentary canal has a simple U-shape, the stomach being situated at the bend.

The most important features of this canal are the salivary glands and the œsophageal cæcum (Pl. X, Fig. 1, *o.c.*). The former consists of two pairs, the one tubular and the other racemose,[2] situated in

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[1] It is strange to find so well known a malacologist as Dall (Bull. Mus. Comp. Zool., vol. xviii. 1889, pp. 152 and 155) still regarding the osphradium as a gill; at least, he speaks of *Aurinia*, one of the Volutidæ, as possessing two well-developed gills, and these can only be the true gill and the osphradium.

[2] Quoy & Gaimard and Bouvier both fell into the error of taking these two pairs of glands for a single pair, and regarding the tubular gland as a posterior continuation of the racemose gland. It has not been deemed necessary to figure these glands in more than one of the animals described, since they do not vary. Their position and shape will be gathered by reference to Figs. 4, 5, and 6.

front of the nerve-collar. The latter pair consists of large, compact, but acinous glands, situated on either side of the œsophagus near the base of the introvert, and communicating with the alimentary canal by a pair of fine ducts, which run parallel to the œsophagus under cover of the thick circular muscle and eventually open into the buccal mass close to the œsophageal aperture. The tubular glands, which are perfectly distinct from these, consist of a pair of slightly coiled muscular tubes, largest at the blind posterior extremities and tapering off in front; they lie below the racemose glands, and their free ends project out beyond these structures; hence Bouvier, following Quoy & Gaimard, mistook them for tubular backward prolongations of the racemose glands. The tubular glands meet in the middle line below the radula-sac, and thence run forward as an extremely fine duct closely bound up with the latter structure, into which the duct opens in front of the odontophore (Fig. 6). The œsophageal cæcum ('Anhang an der Speiseröhre' of Kieferstein; the great fore-gut gland of Haller) is one of the most striking features in the anatomy of *Voluta* and its allies. A blind outgrowth of the œsophagus appears to be present in the majority of the Rhachiglossa behind the nerve-ring, but it nowhere attains such a striking development as it does in the Volutidæ. In *Voluta* this organ has the form of a long coiled muscular tube, of considerably larger size than the œsophagus, into which it opens ventrally just behind the nerve-collar. In the undisturbed condition this organ is found lying coiled up on the top of the œsophagus (Fig. 1, *o.c.*) and presenting a shiny white appearance. Even in quite a small Volute the cæcum, when uncoiled, measured nearly 8 inches in length.

The radula of this form calls for no comment, since it is typically volutoid, consisting of a stout ribbon bearing about 43 large tricuspid teeth, each tooth constituting a transverse row.

The nervous system.—Very little is known of the nervous system of a typical Volute, for Quoy & Gaimard's figures show nothing beyond a nerve-ring, and Bouvier's description and figures, though giving great detail, refer, as already noted, to the genus *Melo*, in which the nervous system differs somewhat from that of *Voluta ancilla*. An examination of Fig. 9 will give a fair idea of the nervous system of this Volute, and it will be at once evident that it is characterized by extreme concentration round the œsophagus. The two cerebral ganglia are closely connected in the middle line, and are still more intimately fused to the pleural ganglia behind and below. The cerebro-pedal and pleuro-pedal connectives are so short and broad that it becomes almost a difficult matter to distinguish between the pedal ganglia on the one hand and the cerebrals and pleurals on the other. The cerebral ganglia give off about four conspicuous nerves, which run forward to the head-lobes, tentacles, and eyes, and also a pair of small nerves which run inward to the buccal ganglia (*b.g.*), the latter, as in other Rhachiglossa, being situated close to the nerve-collar. The pedal ganglia are somewhat abruptly truncated ventrally, and give off numerous nerves to the large foot. From the right pleural ganglion arises an extremely short

pleuro-visceral connective, which almost immediately passes into the supra-intestinal ganglion; in fact, the latter is only just separated by a constriction from the right pleural ganglion. The former ganglion gives off three nerves which supply the osphradium and gill and complete the left half of the visceral loop, and also probably form a dialyneurous connection with a nerve arising from the left pleural, as in *Volutilithes*. The sub-intestinal ganglion (*sb.g.*) is intimately related both to the left and to the right pleural ganglion, i.e. it presents a zygoneurous condition; it gives off two prominent nerves, which run back, and one of them completes the visceral loop.

The nervous system, on the whole, presents a highly specialized condition, having attained almost a maximum amount of concentration, far more so than that seen in *Melo Neptuni* as described by Bouvier, for in that form the supra-intestinal ganglion is separated by a wide interval from the right pleural ganglion. The great development of the pleuro-visceral connective in this species suggests a more primitive condition than that met with in *Voluta ancilla*, unless it is possible for the ganglia after once becoming concentrated to become secondarily dissociated.

2. Neptuneopsis Gilchristi, Sby.

The *external characters* of this Prosobranch, a short account of which has already been published,[1] are not at all suggestive of the Volutidæ; for example, there is a very large functional operculum, an uncommon feature in this family, being only met with in the genera *Volutolyria* and *Lyria*. The head also is unlike that of *Voluta*, since it bears two very large massive tentacles (Fig. 2), the appearance presented being that the head-lobes of *Voluta* had become incorporated in the tentacles. There is a large snout, which in all probability is introvertible, but this region of the specimen was considerably damaged before I received it, so that it was impossible to determine the point with any degree of certainty. The siphon is not so large as in *Voluta*, and is devoid of appendices.

The *pallial complex*, on the other hand, might be that of *Voluta*, the form and relation of the organs composing it being in every respect the same.

The alimentary canal.—Unfortunately the buccal mass was removed before I received the specimen, and in its removal the salivary glands were practically destroyed, one only of the tubular glands being left. From general considerations I feel safe in concluding that these organs would be precisely like those of *Voluta*. The rest of the alimentary canal also might be that of *V. ancilla* (cf. Figs. 1 and 3), though perhaps the œsophageal cæcum is more largely developed in *Neptuneopsis*.

The heart, kidney, and genitalia (♀) call for no comment; like those of *Voluta* they are typically rhachiglossate.

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[1] Sowerby, op. cit.

The *nervous system* (Figs. 11, 13, and 14) of *Neptuneopsis* closely accords with the volutoid type, differing from the latter only in being slightly less compact; thus the commissure connecting the supra-intestinal ganglion with the right pleural is slightly longer than in *Voluta ancilla*, and in a similar way the sub-intestinal ganglion is less completely fused with the pleurals. In this respect *Neptuneopsis* is somewhat intermediate between *Voluta ancilla* and *Melo Neptuni* as described by Bouvier.

In the short summary of the anatomy of the form which I supplied to Mr. Sowerby, and which was published in his original description of this genus, I state that the nervous system of *Neptuneopsis* differed considerably from that of *Voluta*. In making the comparison I was labouring under the belief that Bouvier had described a true Volute, instead of a member of the genus *Melo*. This correction removes the only point of difference between the internal organs of *Neptuneopsis* and of *Voluta*, if the form I have described, *V. ancilla*, be typical of this genus.

3. Volutilithes abyssicola (Ad. & Rve.).

External characters. — The head is slightly compressed dorso-ventrally, and divided anteriorly by a deep median cleft (Fig. 8); these two anteriorly placed head-lobes are intimately related to the opening through which the introvert is protruded; at first sight they might be thought to represent the lips, but this is not the case, the true lips being situated with the mouth at the extremity of the introvert. Each head-lobe is deeply grooved on its outer border, and the inferior margins of these grooves meet ventrally behind the false mouth, in such a manner that these false lips form a V-shaped thickening on the under side of the head (Fig. 8*b*). The tentacles are stout, and related to the upper margins of the grooves in the head-lobes. Behind each tentacle is a short but very stout eye-stalk, bearing a prominent eye on its distal extremity.

The foot is very large, and probably capable of great expansion. There is no operculum. The siphon is long and devoid of appendices. The edge of the mantle is bordered by a single row of low papillæ.

The *pallial complex* is in most respects like that of *Voluta ancilla* or of *Neptuneopsis* (cf. Figs. 1, 3, and 4). The gill and dark-coloured osphradium, being identical in structure, and the anal, genital (♀), and excretory orifices, are similar in position. The only difference, however, is a striking one, and is due to the entire absence of the characteristic hypobranchial gland, a structure present in the majority of the Rhachiglossa.

The alimentary canal. — The buccal mass and radula-sac form a stout muscular mass, occupying the greater part of the introvert (Figs. 4 and 5). As in *Voluta*, two pairs of pre-neural salivary glands are present; one large, branched and whitish pair opens into the œsophagus at its junction with the buccal mass, while the second pair is tubular and yellowish, and unites to form a fine duct, which,

as in *Voluta*, opens into the floor of the buccal mass in front of the odontophore (Fig. 6).

The œsophagus, as in *Voluta* and *Neptuneopsis*, presents that slight enlargement marking the diminution of its muscles, and then passes through the nerve-collar. Behind this structure the œsophagus becomes dilated and convoluted, and then receives the opening of the œsophageal cæcum (*o.c.*); this organ differs considerably in appearance from the similarly named structure in *Voluta* and *Neptuneopsis*, being thin-walled and sacculated; it approximates much more nearly to the œsophageal cæcum of *Buccinum*, and like that organ is of a darkish colour. The stomach and intestine are like those of *Voluta*. The circulatory, excretory, and reproductive systems call for no comment, since they resemble those of the majority of the Rhachiglossa.

The *radula* of *Volutilithes* (Fig. 7) is of special interest, for, like that of *Volutomitra*, at present referred to the Volutidæ, it exhibits three teeth in each transverse row. Of these rows there are about 110, but owing to the small size of the teeth the radula is small and delicate. The central or rhachidian tooth is tricuspid, the three cusps being subequal, and as in *Voluta* attached to a curved base. The lateral teeth are unicuspid, each possessing an oblong base from which a single cusp projects backward; this cusp rises as high as the outer cusps on the central tooth, and is situated near the inner margin of the oblong base.

In seeking for a form with which to compare the radula one naturally turns in the first instance to *Volutomitra*,[1] the only other volutoid genus with a triserial radula. At first glance this seems to be a happy comparison, especially as regards the lateral teeth, which have the form of flattened oblong plates from which springs a very small cusp; the central tooth of *Volutomitra* is, however, very dissimilar to that of *Volutilithes*, being a simple V-shaped tooth, not unlike the peculiar tooth of *Amoria*, a subgenus of *Voluta*, but which is so different from that of the typical Volute, that one is inclined to question the correctness of its systematic position; at any rate, it must be a very specialized form. On the whole I do not think that the radula of *Volutilithes* has much affinity with that of *Volutomitra*, although it is conceivable that the latter genus might have arisen from the former, and in its turn have given origin to *Amoria*.

Professor Gwatkin has kindly looked through his large series of radulæ to see if any form would compare with *Volutilithes*, but is unable to find any radula which at all suggests that of this genus. He is inclined to lay stress on the side teeth, and come to the conclusion that if we can compare the radula of *Volutilithes* with that of any known form it must be with *Mitra*. This conclusion is one which would fit in with the statements made by Fischer in his Manual concerning the genus *Volutomitra*, which he regards as a natural transition between the Volutidæ and Mitridæ. Unfortunately these views are not borne out by a study of the anatomy of these

[1] Troschel: "Das Gebiss der Schnecken," Bd. ii, pl. v, fig. 56.

forms, and from what we know in this respect the Volutidæ and Mitridæ have no connection. Neither should I myself consider that there was any similarity between the radulæ; the only Volute which in its radula suggests the Mitridæ is the genus *Volutolyria*, and from the character of the tooth I should conclude that it had little in common with the forms at present placed in the genus *Voluta*. Personally, with regard to the radula of *Volutilithes*, I would lay stress on the central tooth, which is undoubtedly volutoid, whereas the lateral teeth suggest that they are undergoing reduction, a feature which we might expect to see preserved in a primitive Volute. If we may compare this radula with that of any typical living rhachiglossate, I would suggest a resemblance to the Turbinellidæ and Buccinidæ.

The nervous system.—Owing to the excellent state of preservation of the specimens it was possible to work out the nervous system of *Volutilithes*, in spite of its small size, in much greater detail and with better results than in the very much larger *Voluta*. The arrangement of the ganglia constituting the nerve-collar in the two genera is, however, practically identical, as a comparison of Figs. 9 and 10 will show. It was, moreover, possible to demonstrate the dialyneurous condition on the left side, which was only surmised to be present in *Voluta*. The otocyst also was easily seen, and even the fine nerve connecting it with the cerebral ganglion (Fig. 12). As in other Rhachiglossa, a single large otolith was found within this structure.

Conclusion.

A comparison of the above accounts will show, I think, that while the three forms dealt with differ in some features in their anatomy, yet they so closely resemble one another in so many other points that we are justified in retaining them in one family. *Volutilithes*, the shell of which has long been known, was originally placed in the family Volutidæ on purely conchological grounds. On the other hand, the animal of *Neptuneopsis* was examined at the same time as the shell, and I think if it had not been for a consideration of the radula, and possibly also of other anatomical features, there would have been more hesitation in placing this form in the Volutidæ, since the only volutoid character seen in the shell is the protoconch, whereas the general form of the shell and the absence of characteristic folds on the columella and the presence of a large operculum would have told strongly against its volutoid affinities. Nevertheless, an examination of its anatomy, especially of its nervous system, alimentary canal, with the radula and appended glands, and the pallial complex, shows that this form is undoubtedly a near ally of the genus *Voluta*.

Volutilithes, though unhesitatingly placed with the Volutidæ on conchological grounds, differs from the family more than *Neptuneopsis* does, and whilst from the peculiar character of its salivary glands and the details of its nervous system we should certainly regard it as belonging to that family, yet in the character of its radula, the small size and nature of the œsophageal cæcum, and the absence of

a hypobranchial gland, it stands apart from those other members of the Volutidæ whose anatomy is at present known. The three characters mentioned may, from what we know of prosobranch anatomy, be reasonably regarded as primitive features, and when we remember that the genus *Volutilithes* was originally founded to embrace a number of fossil forms common in the Cretaceous, Eocene, and Oligocene beds, it becomes extremely probable, if the conchological identification be correct, that the form would retain a more primitive organization than the more recently developed genera, such as *Voluta*, *Melo*, etc. Such being the case, I am inclined to regard *Volutilithes* as the living form which stands nearest to the ancestors of the Volutidæ, and one which, while it had acquired or inherited certain of the characteristic features of the Volutidæ, nevertheless retained a number of characters belonging to its less specialized rhachiglossate ancestors.

One difficulty stands in the way of this conclusion, viz. the nervous system of *Melo Neptuni*, in which we find the supra-intestinal ganglion separated by a long interspace from the right pleural. With regard to this point I cannot help thinking that possibly the condition seen in *Melo* is not, after all, a primitive character, since this form is in other respects a highly specialized Volute, and since also in other groups of Prosobranchs the relative degree of proximity between these two ganglia seems to vary, so much so that I believe it is possible for this separation to be at times a new secondary condition arising from a concentrated one, and not a direct inheritance of the primary architænioglossate condition.

From the above remarks it will be gathered that our knowledge of the anatomy of the Volutidæ and of the whole rhachiglossate group is still very meagre, and we must at present regard the classification of these forms as purely provisional. It is extremely probable that we are at present incorporating in the Volutidæ several forms derived from distinct stocks; in other words, this is not a natural family, and in all probability *Volutolyria*, at least, will have to be separated from the other members of the Volutidæ when we know more of its anatomy. Still, one would think that more use might be made of the radulæ by systematists than is at present done, and one has only to look at our textbooks to see what divergent forms are incorporated, not merely in the same family, but in the same genus; thus, in the genus *Mitra* forms exhibiting five totally distinct types of radula are included.

I have not attempted to define the family Volutidæ anatomically, because I consider that we need a great deal more information before such a definition can be possible; but I think that the presence of two pairs of pre-neural salivary glands, one tubular and one grape-shaped, an œsophageal cæcum, the concentrated nervous system, as described above, together with a radula with a tricuspid central tooth (? sometimes unicuspid), will be found to be characteristic of all Volutes.

The importance of a knowledge of the anatomy of any form is well exemplified by such a form as *Neptuneopsis*, and will be still more